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CLIMATIC DRIVERS OF LATITUDINAL VARIATION IN LATE TRIASSIC TETRAPOD DIVERSITY

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Abstract: The latitudinal biodiversity gradient (LBG), the increase in biodiversity from the poles to the equator, is one of the most widely recognized global macroecological patterns, yet its deep time evolution and drivers remain uncertain. The Late Triassic (237–201 Ma), a critical interval for the early evolution and radiation of modern tetrapod groups (e.g. crocodylomorphs, dinosaurs, mammaliamorphs), offers a unique opportunity to explore the palaeolatitudinal patterns of tetrapod diversity since it is extensively sampled spatially when compared with other pre-Cenozoic intervals, particularly at lower palaeolatitudes. Here, we explore palaeolatitudinal patterns of Late Triassic tetrapod diversity by applying sampling standardization to comprehensive occurrence data from the Paleobiology Database (PBDB). We then use palaeoclimatic model simulations to explore the palaeoclimatic ranges occupied by major tetrapod groups, allowing insight into the influence of palaeoclimate on the palaeolatitudinal distribution of these groups. Our results show that

Late Triassic tetrapods generally do not conform to a modern-type LBG; instead, sampling-standardized species richness is highest at mid-palaeolatitudes. In contrast, the richness of pseudosuchians (crocodylians and their relatives) is highest at the palaeoequator, a pattern that is retained throughout their subsequent evolutionary history. Pseudosuchians generally occupied a more restricted range of palaeoclimatic conditions than other tetrapod groups, a condition analogous to modern day reptilian ectotherms, while avemetatarsalians (the archosaur group containing dinosaurs and pterosaurs) exhibit comparatively wider ranges, which is more similar to modern endotherms, such as birds and mammals, suggesting important implications for the evolution of thermal physiology in dinosaurs.

Key words: Late Triassic, diversity, latitudinal biodiversity gradient, Tetrapoda, thermal physiology, general circulation palaeoclimatic model.

THE latitudinal biodiversity gradient (LBG), characterized by an increase in species richness towards the equator, is one of the most widely recognized global patterns in macroecology (Willig *et al.* 2003; Hillebrand 2004). Though the LBG has been extensively documented in modern terrestrial vertebrate faunas, its evolution and drivers through deep time remain uncertain. The fossil record offers an exceptional deep-time perspective on the LBG, and previous work suggests that a modern-type gradient has not been persistent in terrestrial tetrapods throughout the Phanerozoic, instead varying widely across time and taxonomic groups (Rose *et al.* 2011; Mannion *et al.* 2012, 2014; Marcot *et al.* 2016; Brocklehurst *et al.* 2017). Several hypotheses have been proposed to explain the modern LBG, some relating to the age and areal extent of modern-day tropical regions (see Chown & Gaston 2000; Mittelbach *et al.* 2007, Mannion *et al.* 2014) and others regarding speciation rates and biotic influences

(Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Roy & Goldberg 2007; Soria-Carrasco & Castresana 2012). However, climate is often regarded as the primary driver of latitudinal variation in diversity through time (Powell 2007; Erwin 2009; Archibald *et al.* 2010; Rose *et al.* 2011; Marcot *et al.* 2016; Kröger 2017).

The Late Triassic (237–201 Ma) presents an exceptional opportunity to explore palaeolatitudinal gradients in terrestrial diversity. During the Late Triassic, both the climate and continental configuration were very different to the present day, with generally much warmer temperatures, an absence of ice at the poles, and the configuration of the continents into the supercontinent Pangaea. The Late Triassic was a critical interval in the evolutionary history of tetrapods (four-limbed vertebrates); by this time the early radiations of several major modern lineages such as mammaliamorphs (Ruta *et al.* 2013), crocodylomorphs (Butler *et al.* 2011; Irmis *et al.* 2013), dinosaurs

(Benton 1983; Brusatte *et al.* 2008, 2010; Langer *et al.* 2010), lissamphibians (Stocker *et al.* 2019) and lepidosaurs (Cleary *et al.* 2018) were underway. Previous studies have recognized palaeolatitudinal variation in Late Triassic tetrapod faunas (Tucker & Benton 1982; Shubin & Sues 1991; Irmis *et al.* 2007; Ezcurra 2010; Irmis 2011; Whiteside *et al.* 2011, 2015). However, this palaeolatitudinal variation and its relationship with global palaeoclimatic conditions has not been extensively explored across all tetrapods, largely due to the absence of a comprehensive dataset of global tetrapod occurrences and palaeoclimate reconstructions (model or proxy data) with sufficient temporal and spatial coverage to examine and compare patterns across large time intervals. Past studies have relied on indirect comparisons between temporal trends in palaeolatitudinal diversity and trends in palaeoclimate, or used palaeolatitude as a proxy for global climate conditions (Powell 2007; Marcot *et al.* 2016). Even in studies of the modern-day LBG, latitude is often used as a proxy for numerous interacting environmental variables, such as temperature and seasonality (Willig *et al.* 2003; Hillebrand 2004).

Further difficulty arises when examining the LBG through time, because variation in spatial and temporal sampling strongly influence the fossil data, particularly at the global scale; the presence or absence of a latitudinal diversity gradient in certain time intervals or in selected fossil groups cannot be confidently attributed to any abiotic or biotic factor without considering biases in sampling. Additionally, debate continues over whether it is possible to decipher genuine latitudinal gradients in diversity from the fossil record, or whether the apparent patterns in latitudinal species richness are artefacts of geographical shifts in sampling efforts through time (Close *et al.* 2017; Fraser 2017). The Late Triassic has also been extensively sampled across palaeolatitudes (Dunne *et al.* (2020, fig. S1). This is particularly true for sites at low-palaeolatitudes, for example in south-western USA (Long & Murry 1995), but also at mid-palaeolatitudes, for example in Germany (Deutsche Stratigraphische Kommission 2005), as well as at higher palaeolatitudes, such as in Argentina's Ischigualasto Formation (Martínez *et al.* 2012), and the Elliot Formation of southern Africa (Knoll 2005).

Here, we examine palaeolatitudinal variation in Late Triassic tetrapod diversity, using fossil occurrence data from the Paleobiology Database (PBDB) and sampling standardization to mitigate the effects of heterogeneous spatial sampling. Then, combining this occurrence data with palaeoclimate reconstructions from a spatially-explicit general circulation climate model, HadCM3L (Valdes *et al.* 2017), we assess the relationship between latitudinal species richness and both sampling and palaeoclimatic conditions. Finally, we explore the palaeoclimatic

conditions occupied by major tetrapod groups and discuss how these ranges might relate to the evolution of thermal physiology (i.e. ectothermy and endothermy).

MATERIAL AND METHOD

Fossil occurrence data

Global occurrences of tetrapod species from all stages of the Late Triassic (Carnian–Rhaetian; 237–201.3 Ma) were downloaded from the PBDB (<https://paleobiodb.org>). Before download, the occurrence data were checked against the current published literature for completeness and missing occurrences were added. Data preparation and statistical analyses were conducted within R 3.5.2 (R Core Team 2018). The occurrence dataset was filtered to remove marine and flying taxa, as well as taxonomically indeterminate occurrences (i.e. those that could not be confidently assigned to a valid genus or species). Trace fossil occurrences were also removed from the dataset, as they represent a distinct type of data that is not the focus of this study and due to the biological non-equivalence of trace fossils and body fossils (i.e. trace fossils are not easily allied with body fossil species and an organism can produce multiple traces). The final cleaned dataset comprises 1382 unique tetrapod occurrences, representing 401 species belonging to 325 genera, from 676 collections (= fossil localities).

Latitudinal sampling and species diversity

For the following analyses of sampling and diversity patterns, the data were placed in palaeolatitudinal bins, which were set at 10-degree intervals (with the exception of the most poleward bin in each hemisphere, which was set at ± 50 – 90° due to the very sparse sampling at these high palaeolatitudes). Palaeolatitudes are assigned to collections (= fossil localities) by the PBDB using the chronostratigraphic information provided by the data enterer and the GPlates palaeogeographic rotation model (Wright *et al.* 2013). For the terrestrial Late Triassic, these palaeolatitudes are generally only available at the stage level, which means that continental drift (e.g. the movement of Pangaea northward during the Late Triassic) can only be captured at this coarse level. This is because the maximum and minimum time interval fields of the PBDB only accept formally defined chronostratigraphic subdivisions, and most terrestrial Late Triassic localities in the Database cannot or have not been assigned with certainty to substage level intervals.

We first present face-value (= raw, uncorrected or observed) species richness at global and local spatial scales; however, we do so with the proviso that face-value

diversity counts may be highly misleading, and instead focus our interpretation on diversity patterns produced using coverage-based sampling standardization. Global (gamma scale) face-value diversity curves were computed using sampled-in-bin counts of specifically determinate occurrences. Counts of collections, formations, and occupied equal-area grid cells (50 km spacing, computed using the *dggridR* package in R; Barnes *et al.* 2018), were used as proxies for sampling effort. To look at temporal changes in sampling, the data were further divided into subsets that were generally equal in length, based on the stratigraphic ages of individual formations outlined in Button *et al.* (2017); the ‘early Late Triassic’ (approximately Carnian to early Norian) and ‘late Late Triassic’ (approximately late Norian to Rhaetian).

We estimated local richness (alpha diversity) by counting the total number of species per collection (= fossil locality) for: (1) all tetrapods; (2) Archosauromorpha; (3) Pseudosuchia (including phytosaurs *sensu* Ezcurra 2016); (4) Avemetatarsalia (*sensu* Nesbitt *et al.* 2017); (5) Synapsida; and (6) Temnospondyli. The relationships between these groups can be seen in Figure 1. These counts included not only occurrences determined at species level but also those indeterminate at species level (e.g. genera not assigned to a species) that must logically represent distinct species according to the taxonomic hierarchy of the PBDB, following Close *et al.* (2019). Prior to the interpretation of these results, we tested for any influence of well-sampled sites on estimates of local richness by removing collections with more than ten distinct occurrences. Additionally, we tested the effect of literature biases by removing occurrences originating in large monographic publications (i.e. Long & Murry 1995).

We used coverage-based sampling standardization to estimate global palaeolatitudinal diversity patterns, via the R package *iNEXT* (v. 2.0.19; Hsieh *et al.* 2016), following the procedure outlined by Dunne *et al.* (2018). Coverage-based sampling standardization uses the concept of frequency-distribution coverage, a measure of sample completeness that can be accurately and precisely estimated using Good’s *u* (Good 1953) to make fair comparisons of diversity between assemblages that may be sampled to very different levels of intensity. This method was introduced by Alroy (Alroy 2010a, b, c, 2014) under the name ‘shareholder quorum subsampling’ (SQS), using an algorithmic approach. The analytical implementation of SQS in *iNEXT* yields confidence intervals and allows coverage-based extrapolation (using the Chao1 estimator), in addition to interpolation (1/4 subsampling). The data were rarefied by collection (= fossil locality), by analysing incidence-frequency matrices of the occurrence data. Extrapolated estimates were limited to no more than twice the observed sample size (as recommended by Hsieh *et al.* 2016). We computed coverage-standardized richness at

both species and genus level for the largest taxonomic groups mentioned above: (1) all tetrapods; (2) Archosauromorpha; and (3) Pseudosuchia (see Fig. 1). Coverage-standardized richness estimates were not possible for other groups due to insufficient data.

Palaeoclimate reconstructions

To investigate the relationship between palaeoclimatic conditions and patterns of diversity during the Late Triassic, we used an ensemble of readily comparable palaeoclimate model simulations spanning the Late Triassic. We used a general circulation model (GCM) HadCM3L, specifically HadCM3LB-M2.1E (Valdes *et al.* 2017), which is a fully coupled atmosphere–ocean GCM incorporating the MOSES 2.1 land surface scheme, which includes a fully interactive vegetation model TRIFFID (top-down representation of interactive foliage and flora including dynamics). The spatial resolution of the model is 2.5° latitude by 3.75° longitude with 19 vertical levels in the atmosphere and 20 depth levels in the ocean (Valdes *et al.* 2017). The simulations performed here follow the Lunt *et al.* (2016) standardized experimental methodology including an internally consistent set of palaeogeographic reconstructions created by Getech Plc. using the methods of Markwick & Valdes (2004) allowing model simulations to be self-consistent across geological time. The palaeodigital elevation models (topography, bathymetry, ice sheets) used as the model boundary conditions are derived from palaeogeographic proxy reconstructions using an extensive geologic database of tectonics, structures, and depositional environments (Lunt *et al.* (2016)). HadCM3LB-M2.1E has demonstrated good skill in predicting global and regional scale climate patterns against in-situ observations and proxy reconstructions not only in the present (Valdes *et al.* 2017), but crucially in the past as well (Farnsworth *et al.* 2019a). In addition, the model has been successfully used in several niche modelling studies (Fenton *et al.* 2016; Saupe *et al.* 2019) and demonstrated good ability in predicting deep-time species distributions (Chiarenza *et al.* 2019).

One simulation was run per geological stage of the Late Triassic (Carnian, Norian and Rhaetian), using stage-specific palaeogeography, a stage-appropriate reduced solar constant (Gough 1981) and an atmospheric CO₂ concentration of 1120 ppmv (or 4× pre-industrial CO₂, representing a generic ‘greenhouse world’), which is within the range of uncertainty for the entire Late Triassic (Foster *et al.* 2017). These simulations were run for ~1400 model years to ensure the climate system had approached equilibrium in the atmosphere and upper ocean. Although not long enough to allow the deep ocean to reach full equilibrium, it has been shown that the large-scale

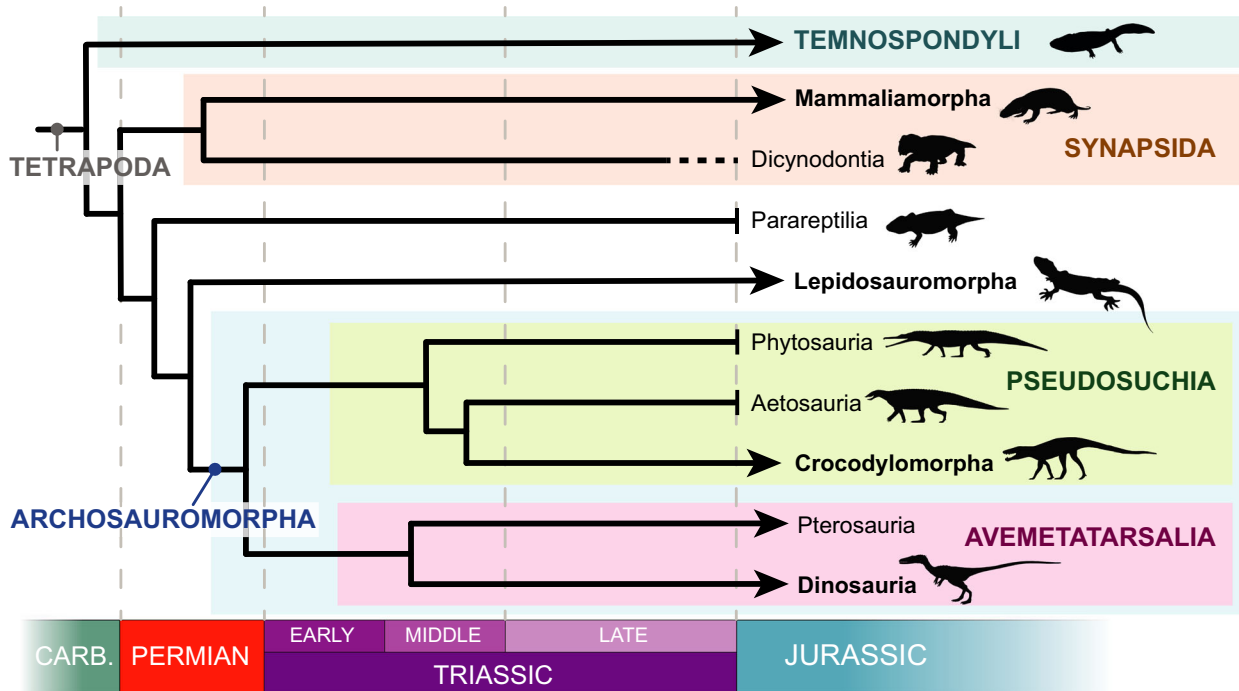


FIG. 1. Simplified schematic showing the relationships between the six tetrapod groups used in this study. Representative clades of each group are shown, with the lineages that lead to modern tetrapod groups denoted with bold text, i.e. modern mammals (Mammaliamorpha), modern lepidosaurs (Lepidosauromorpha), modern crocodylians (Crocodylomorpha), and birds (Dinosauria). Silhouettes from <http://www.phylopic.org/>; see Acknowledgments for details.

circulation does not change substantially thereafter as the deep ocean equilibrates (Farnsworth *et al.* 2019b). However, future work is required to spin-up these simulations to a more closely equilibrated state to remove this potential source of uncertainty. At present, simulations are only available at the level of geological stages, rather than finer scale time intervals. There is a high degree of uncertainty in $p\text{CO}_2$ proxy reconstructions during the Late Triassic with values as low as ~400 ppm during the Carnian and as high as ~2900 ppm in the Norian (Foster *et al.* 2017). This means we are not sampling the impact of the potential range of secular climate change across the Late Triassic. However, the strength of our approach is that we can isolate the impact of changing palaeogeography through the Late Triassic and its impact on LBGs. Future work should focus on investigation of this secular climate change signal as a result of varying CO_2 .

From the model output, we extracted four of the most commonly used palaeoclimatic variables in studies of the links between palaeodiversity and palaeoclimate: mean annual surface temperature (MAT), mean annual precipitation (MAP), and seasonal variations of both measures derived from the difference between the mean warmest month and the mean coldest month and the mean wettest month and the mean driest month, respectively. These variables are the average value of the rotated model grid

cell plus all adjacent 'land' grid cells, as opposed to single values for individual model grid cells (subject to some degree of numerical 'noise'). Values for MAT, MAP, and seasonal variations of each were attached to fossil occurrences by taking the modern coordinates of the collection (= fossil locality) they are assigned within the PBDB and rotating these coordinates back to the stage-appropriate palaeocoordinates in the Getech plate model. For fossil occurrences that were assigned to collections spanning two stages (due to stratigraphic uncertainty e.g. Carnian–Norian), the mean of each palaeoclimatic variable was calculated. Those spanning more than two stages were discarded from the dataset to remove any influence of temporal uncertainty.

Drivers of diversity and palaeoclimatic ranges

Generalized least-squares (GLS) is a multiple regression technique that does not assume independence of data series (or points within a data series), which has previously been used in palaeontological studies to examine relationships between multiple time series variables simultaneously (Hunt *et al.* 2005; Benson & Butler 2011; Mannion *et al.* 2012; Cleary *et al.* 2018; de Celis *et al.* 2019). Following the approach of Benson & Butler (2011) we used GLS to

examine the relationship between palaeolatitudinal species richness, sampling (tetrapod-bearing collections), and palaeoclimate (MAT and MAP). The best models (i.e. combinations of explanatory variables) were identified using the AIC for small sample sizes (AICc; Hurvich & Tsai 1989), which selects the model(s) that explain the highest proportion of variation in global species richness with the fewest explanatory variables. All GLS and associated tests were performed in R with the package nlme (v. 3.1.137; Pinheiro *et al.* 2019).

We first examined the relationship between face-value palaeolatitudinal species richness, sampling, and palaeoclimate across palaeolatitude, by calculating the total number of tetrapod species and tetrapod-bearing collections, as well as the mean annual temperature (MAT) and precipitation (MAP) for each 10° palaeolatitudinal bin, outlined above. Next, we examined the relationship between coverage-rarified tetrapod species richness and palaeoclimate (MAT and MAP), by extracting the coverage-rarified estimates from the iNEXT output for each 10° palaeolatitudinal bin. Autoregressive models of order zero, one or two were fit to combinations of explanatory variables used to predict palaeolatitudinal species richness, and the best order determined by likelihood ratio tests, implemented using the `gls` function of nlme. Species richness, sampling proxies and palaeoclimatic variables were log-transformed prior to analysis to ensure normality and homoskedasticity of residuals (Jarque & Bera 1980). Likelihood-ratio based pseudo- R^2 values were calculated separately using the `r.squaredLR` function of the R package MuMIn (v. 1.43.10; Barton 2019).

Finally, to explore the full range of palaeoclimatic conditions (MAT, MAP, and seasonal variations of both) occupied by each of the five major tetrapod groups, we constructed boxplots using the palaeoclimatic values assigned to fossil occurrences as described above.

RESULTS

Diversity and sampling

Sampling of Late Triassic tetrapods varies across palaeolatitudes (Fig. 2A), with sampling greatest in the northern palaeo-hemisphere at low and mid-palaeolatitudes (0–40°). There is a complete absence of sampling between 0–30° in the southern palaeo-hemisphere, an area of land that is today covered in part by the Sahara Desert in Africa and Amazon rainforest in South America (Fig. 2B). However, in the southern palaeo-hemisphere there is a level of sampling at mid-palaeolatitudes (30–40°) that is analogous to the corresponding palaeolatitudes in the northern palaeo-hemisphere. Visual inspection shows that face-value species richness closely

tracks proxies for sampling effort (counts of collections, formations, and occupied equal-area grid cells) across most palaeolatitudinal bins, except in the 10–20°N bin where collection count far exceeds total species, indicating extensive sampling within this region (primarily the south-western USA). Temporal variation in sampling is also evident between the early Late Triassic and late Late Triassic (Dunne *et al.* 2020, fig. S2A, B) but continues to be high during both sub-intervals in the 10–20°N bin. Values of Good's u (an indication of 'coverage', or how well-sampled a bin is) generally remain within the range of 0.5–0.8 across all sampled palaeolatitudinal bins, both when the Late Triassic is treated as a single interval and when it is divided (Dunne *et al.* 2020, fig. S2C–E).

Local richness, or alpha diversity, potentially provides important insights into latitudinal patterns of diversity, as alpha diversity estimates may be less strongly affected by biases in sampling that can confound global diversity compilations (Close *et al.* 2019). Across the entire Late Triassic, tetrapod local richness is highest at low palaeolatitudes, mostly in the northern palaeo-hemisphere (Fig. 3A). Most of the localities with the highest species richness lie in the northern palaeo-hemisphere (between 5° and 35°) and correspond to well-sampled localities in Texas and south-western USA (Fig. 3A; Dunne *et al.* 2020, table S1). The richest southern palaeo-hemisphere locality lies in Brazil (Faxinal do Soturo, of Norian age), yet this locality contains less than half the richness of the richest localities in the northern palaeo-hemisphere (Fig. 3A; Dunne *et al.* 2020, table S1). For both Archosauromorpha and Pseudosuchia, local richness is highest at low palaeolatitudes, between 0° and 15° in the northern palaeo-hemisphere (Fig. 3B, C), and the signals for the two groupings are highly similar. There is no clear palaeolatitudinal signal in the local richness of both Avenetatarsalia (Fig. 3D) and Temnospondyli (Fig. 3F), with richness being equally high at both mid (30–40° North and South) and low (0–15° North) palaeolatitudes. Synapsid local richness is highest at mid-palaeolatitudes (30–40°) in both palaeo-hemispheres (Fig. 3E). One locality, Saint Nicholas de Port, France, contains notably higher richness than almost any other locality (Figs 3A, 4E; Dunne *et al.* 2020, table S1). This locality has yielded an abundant microfauna through intensive sampling using screenwashing, including numerous mammaliaform teeth that are rare in most Triassic sites (Debuysschere *et al.* 2015). Screenwashing has also been used at a number of sites in south-western USA, although generally yielding somewhat lower diversity microfaunas, suggesting environment or temporal differences. Screenwashing may however partially explain the high richness of some sites in this region such as the Placerias Quarry (Kaye & Padian 1994).

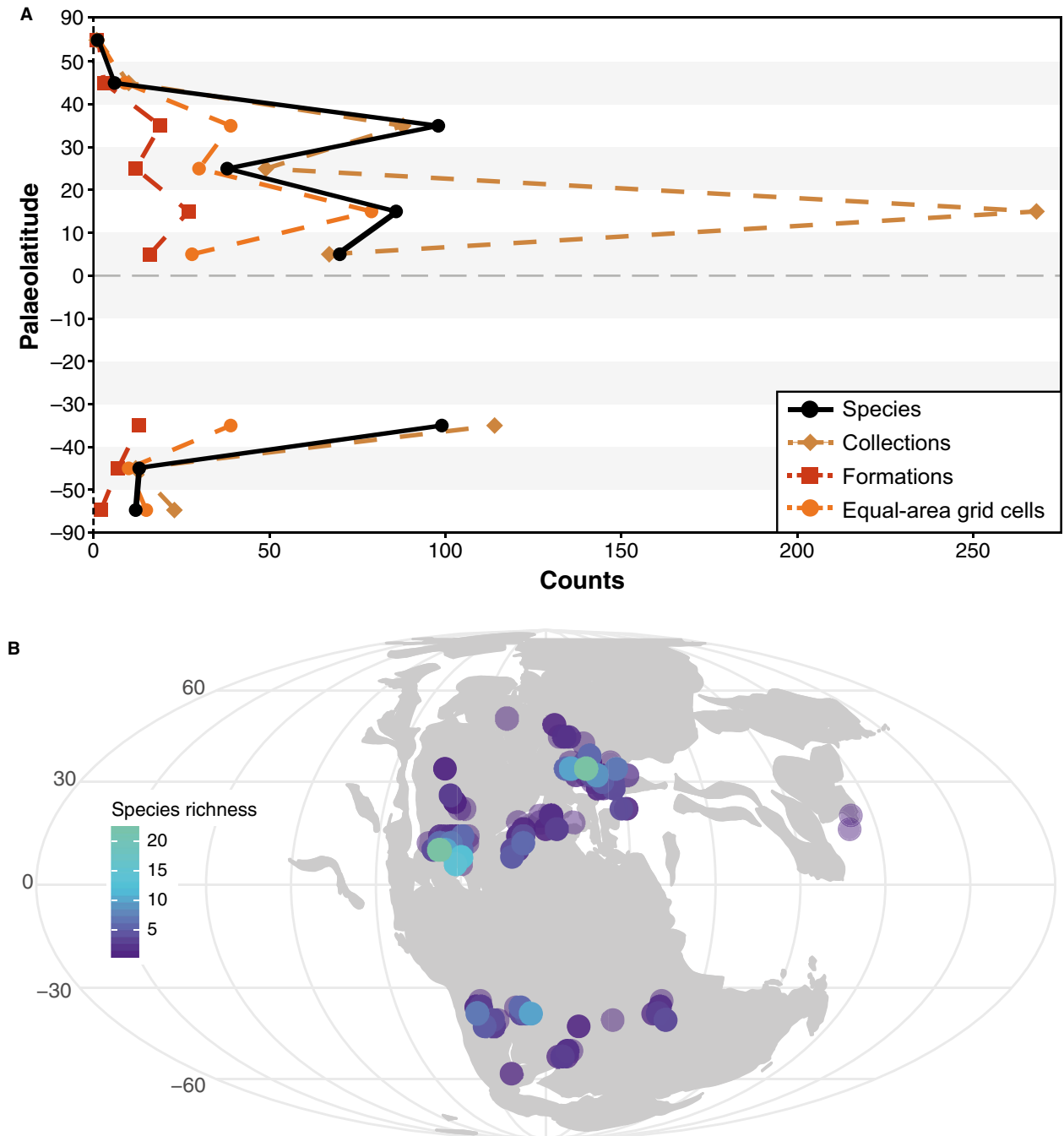


FIG. 2. Patterns of raw or observed species richness and sampling. A, patterns of raw species richness and sampling in the Late Triassic; species richness is highest between 30° and 40° palaeolatitude, both north and south of the palaeoequator. B, palaeogeographical map of fossil localities during the Late Triassic; colour corresponds to total number of species at each site; palaeogeographic configuration is based on that of approximately 220 Ma.

Coverage-standardized estimates of species and genus richness across palaeolatitudes for the entire Late Triassic suggest that diversity was highest at mid-palaeolatitudes for all tetrapods (Fig. 4A; Dunne *et al.* 2020, fig. S3A). This pattern is also evident for archosauromorphs (Fig. 4B; Dunne *et al.* 2020, fig. S3B), but pseudosuchian

richness was highest at lower palaeolatitudes (Fig. 4C). Non-pseudosuchian archosauromorphs (i.e. non-archosaurian archosauromorphs and avemetatarsalians) also displayed highest coverage-rarified genus richness at mid-palaeolatitudes, further suggesting that the signal of high palaeoequatorial richness was primarily driven by

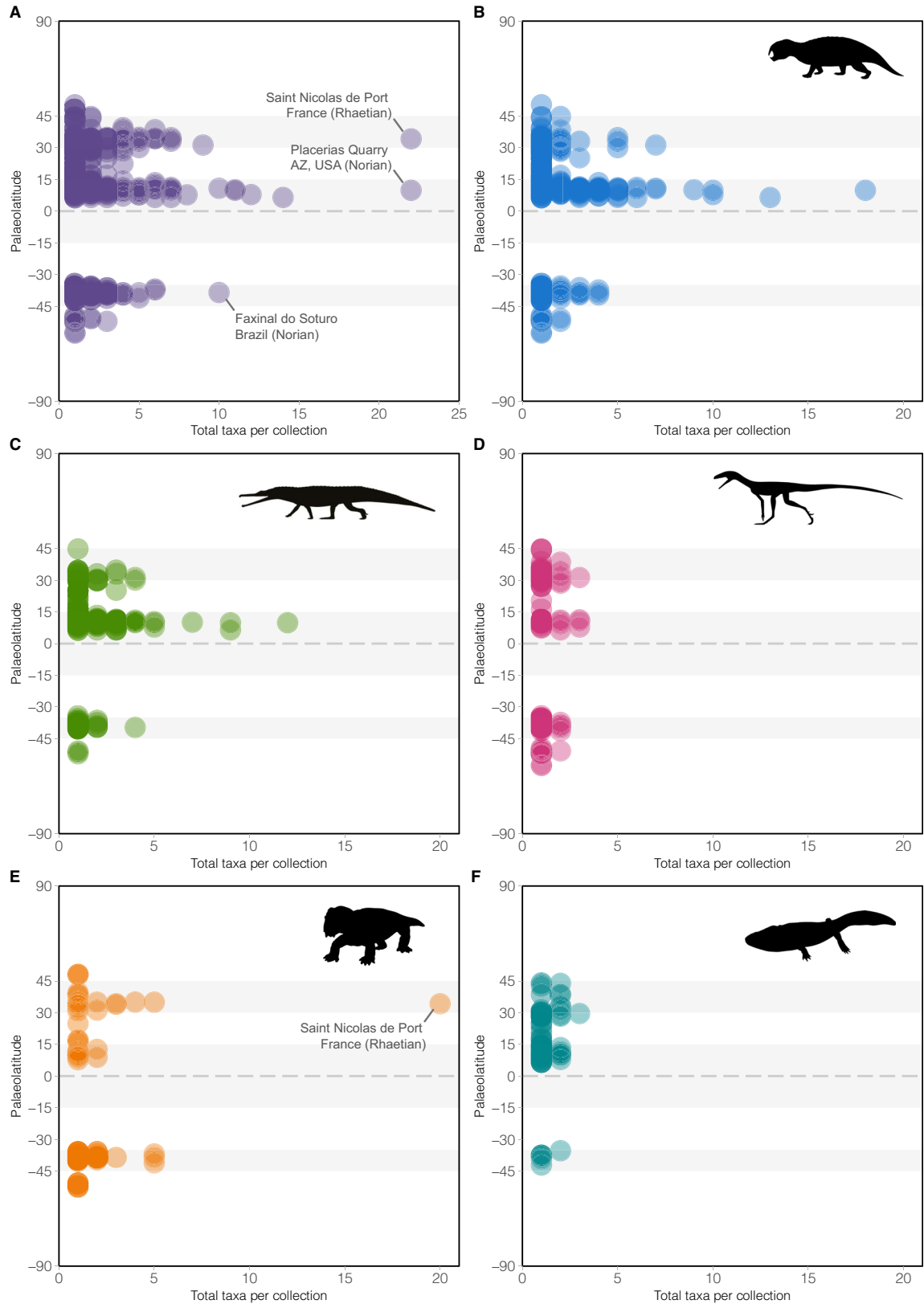


FIG. 3. Total local richness (alpha diversity) for the entire Late Triassic. A, all tetrapods. B, Archosauromorpha. C, Pseudosuchia. D, Avemetatarsalia. E, Synapsida. F, Temnospondyli. Silhouettes from <http://www.phylopic.org/>; see Acknowledgments for details.

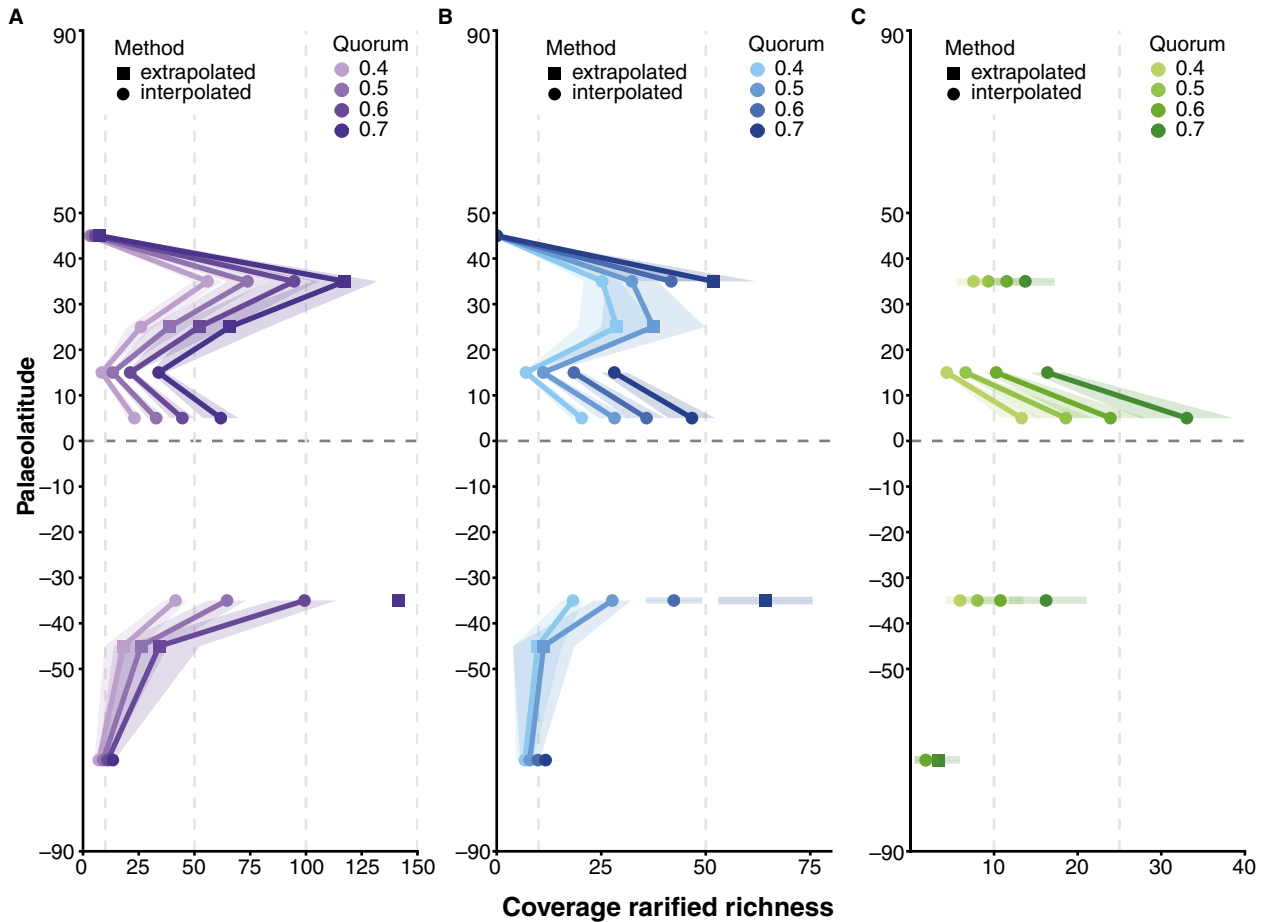


FIG. 4. Coverage-rarified species richness for: A, Tetrapoda; B, Archosauromorpha; C, Pseudosuchia; across all latitudes (using 10° latitudinal bins), showing estimates at different levels of quorum (0.4–0.7).

pseudosuchians (Dunne *et al.* 2020, fig. S3). Coverage was too low for avemetatarsalian, synapsid, and temnospondyl species and genera to obtain estimates of coverage-standardized richness. However, from estimates of archosauromorph and pseudosuchian coverage-standardized richness, it is possible to visually infer that the pattern of high richness at mid-palaeolatitudes is largely driven by non-pseudosuchian archosauromorph taxa, i.e. primarily by avemetatarsalians.

Drivers of diversity and palaeoclimatic ranges

Using palaeoclimatic reconstructions from the general circulation model (GCM) HadCM3L (see Fig. 5), we explored the relationship between diversity, sampling patterns and palaeoclimatic conditions. GLS analysis indicates that face-value (= raw, uncorrected) latitudinal species richness is best explained by a regression model featuring only tetrapod-bearing collections (TBCs), a proxy for sampling (Tables 1, 2). This model accounts for

99% AIC weight, indicating overwhelming support for this over the other models that feature palaeoclimate. It is not possible to clearly distinguish the three best models based on AIC scores, and each of these models contains sampling as an explanatory variable. Likelihood ratio tests between the best two models (Dunne *et al.* 2020, table S3) suggest that adding palaeoclimate variables to the model results in only trivial gains to its explanatory power, and that face-value latitudinal species richness is explained by the model containing only TBCs. Examination of the relationship between coverage-rarified species richness and palaeoclimate reveals that neither MAT nor MAP are better than the null model at predicting coverage-rarified species richness (Table 3). However, MAT and MAP are strongly correlated with coverage-rarified species richness (Table 4), indicating some relationship between diversity and palaeoclimate.

Boxplots illustrating the palaeoclimatic ranges occupied by the major tetrapod groups show that the majority of Late Triassic tetrapods occupy areas that are warm (mean MAT value = 27°C) and have low seasonal variation in

both temperature and precipitation (Fig. 6). Archosauromorpha, as the largest tetrapod clade that contains both Pseudosuchia and Avemetatarsalia, predictably occupies similar palaeoclimatic ranges to all tetrapods (Fig. 6). The majority of pseudosuchians occupy hotter areas (a mean MAT of 31°C, compared with a tetrapod mean of 27°C), with the least seasonal variation in both temperature and

precipitation with respect to other groups (Fig. 6). However, the mean annual precipitation of areas occupied by pseudosuchians falls within the general range of other non-pseudosuchian archosauromorphs (Fig. 6B). Avemetatarsalians and synapsids in general are more abundant in areas with lower mean annual temperatures than other tetrapods (Fig. 6A). These two groups also

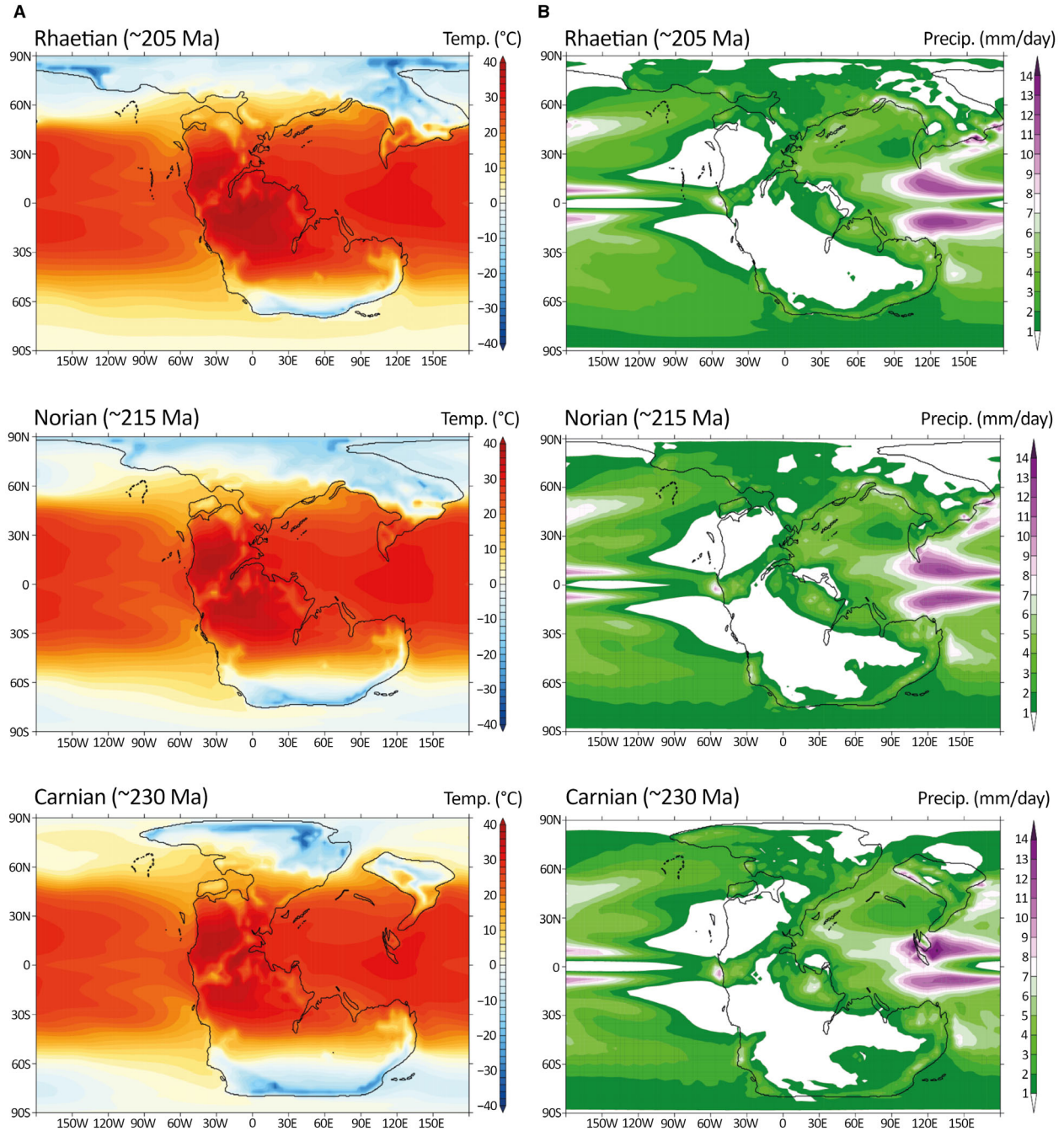


FIG. 5. Palaeogeographic maps for each stage of the Late Triassic displaying: A, global mean annual temperature (in °C); B, mean annual precipitation (in mm/day) from the general circulation model, HadCM3L. Estimates of mean annual precipitation below 1 mm/day have been masked out (i.e. coloured white).

TABLE 1. Summary of model fits to palaeolatitudinal face-value species richness (where the data was assembled into 10° palaeolatitudinal bins), in order of AICc.

Regression model	R ²	Log likelihood	AICc	AIC weight
TBCs	0.932	−3.090	24.179	0.990
TBCs + MAP	0.941	−2.457	34.915	0.005
TBCs + MAT	0.940	−2.519	35.038	0.004
MAT	0.630	−10.718	39.437	0.000
Null model	0.165	−14.376	39.551	0.000
MAP	0.502	−12.048	42.096	0.000
MAT + MAP	0.833	−7.145	44.290	0.000
TBCs + MAT + MAP	0.954	−1.336	56.671	0.000

N = 8 palaeolatitudinal bins; MAP, mean annual precipitation; MAT, mean annual surface temperature; TBCs, tetrapod-bearing collections.

more commonly occupy areas with greater seasonal variation in both temperature and precipitation (Fig. 6C, D). Synapsids generally occupy drier areas (those with the lower MAP) than other tetrapods. Finally, temnospondyls occur in areas with generally higher temperatures, but with low seasonal variation in temperature (Fig. 6A, C) and similar precipitation conditions to archosauromorphs.

DISCUSSION

Despite the Late Triassic interval being one of the most extensively spatially sampled intervals during the time of Pangaea (Fig. 2; Dunne *et al.* 2020, fig. S1) sampling still has a strong influence over the diversity patterns recovered. This is demonstrated by face-value species richness

closely tracking the number of tetrapod-bearing collections, formations and sampled equal-area grid cells across all palaeolatitudes (Fig. 2A). The amount of sampling varies markedly, both spatially across palaeolatitudes (Fig. 2B) and also temporally between the early and late Late Triassic (Dunne *et al.* 2020, fig. S2). These peaks in sampling correspond closely with present-day geographic regions that contain important, extensively-studied fossil localities, for example, localities in the Chinle Formation in south-western USA (low-palaeolatitudes) and in the Caturrita and Santa Maria formations of southern Brazil (mid-palaeolatitudes), which have yielded important fossil specimens that have contributed significantly to the understanding of early dinosaur evolution (Irmis *et al.* 2011; Müller *et al.* 2015; Langer *et al.* 2018). Investigations of local richness (alpha diversity) offer a way to at least partially circumvent many sampling biases that confound regional and global palaeodiversity curves (Close *et al.* 2019). Late Triassic tetrapod local richness is greatest at low and mid-palaeolatitudes, a pattern driven primarily by well-sampled sites (Dunne *et al.* 2020, table S1) but nonetheless affording an insight into the potential level of richness at regional scales (Fig. 3). The only tetrapod group to have high local richness exclusively at mid-palaeolatitudes is Synapsida (Fig. 3), which potentially indicates a difference in the environmental or climatic constraints on the distribution of archosauromorph and synapsid species.

While the above measures indicate that face-value species richness for tetrapods was highest at low-palaeolatitudes, sampling-standardized estimates reveal a more nuanced picture. Estimates of coverage-rarified richness suggest that tetrapod species richness overall peaked at mid-palaeolatitudes, unlike the modern LBG (Fig. 4). This pattern is evident in both palaeo-hemispheres, despite relatively poor sampling in the southern palaeo-

TABLE 2. Summary of explanatory variables within the GLS multiple regression models for palaeolatitudinal face-value species richness as indicated in Table 1.

Regression model	Intercept			Sampling (TBCs)			MAT			MAP		
	Slope	SE	p	Slope	SE	p	Slope	SE	p	Slope	SE	p
TBCs	0.150	0.326	0.659	0.933	0.089	<0.001	—	—	—	—	—	—
TBCs + MAP	1.364	0.963	0.206	0.853	0.107	<0.01	—	—	—	−1.047	0.786	0.231
TBCs + MAT	−0.416	0.603	0.516	0.786	0.146	0.002	0.360	0.296	0.270	—	—	—
MAT	−1.473	1.217	0.266	—	—	—	1.626	0.402	0.005	—	—	—
Null model	2.962	0.764	0.005	—	—	—	—	—	—	—	—	—
MAP	7.391	1.928	0.006	—	—	—	—	—	—	−4.676	2.053	0.057
MAT + MAP	1.463	1.356	0.322	—	—	—	1.474	0.266	0.002	−2.829	0.956	0.025
TBCs + MAT + MAP	1.013	0.972	0.345	0.672	0.158	0.008	0.394	0.278	0.216	−1.278	0.771	0.158

Significant values are in **bold**.

MAP, mean annual precipitation; MAT, mean annual surface temperature; TBCs, tetrapod-bearing collections.

TABLE 3. Summary of model fits to palaeolatitudinal coverage rarified species richness (quorum level = 0.4) in order of AICc value.

Regression model	R ²	Log likelihood	AICc	AIC weight
Null model	0.098	−9.327	30.655	0.803
MAT	0.568	−6.376	34.085	0.145
MAP	0.412	−7.406	36.146	0.052
MAT + MAP	0.813	−3.040	46.079	0.000

N = 7 palaeolatitudinal bins.

MAP, mean annual precipitation; MAT, mean annual surface temperature; TBCs, tetrapod-bearing collections.

hemisphere (although with the caveat that there is no sampling, and therefore no estimates available for coverage-rarified richness, at low-palaeolatitudes (0–30°) of the southern palaeo-hemisphere). The overall palaeolatitudinal pattern for tetrapod diversity appears to be driven by higher mid-palaeolatitude diversity in non-pseudosuchian taxa, namely non-pseudosuchian basal archosauromorphs, avemetatarsalians (including dinosaurs) and synapsids (including mammals). This suggests that the modern-type LBG did not exist at the beginning of the evolutionary histories of these major animal groups. Previous work found a palaeotemperature peak in dinosaur diversity throughout the evolutionary history of the group (Mannion *et al.* 2012). Conversely, pseudosuchians (crocodilians and their relatives) exhibit a modern-type gradient in diversity, and this pattern has been found to have been retained throughout their entire evolutionary history (Mannion *et al.* 2015).

Using palaeoclimate reconstructions from the GMC HadCM3L (see Fig. 6), we were able to explore the range of palaeoclimatic conditions occupied by major tetrapod groups. Generally, each group occupies the complete range of each palaeoclimatic variable (Fig. 6), demonstrating an overlap in realized niches. The majority of species in each group occupy generally warm conditions with low seasonal variability, which is consistent with the conditions found at mid-palaeolatitudes (Fig. 6).

Pseudosuchia were the most constrained group in terms of the range of palaeoclimatic conditions occupied, preferring warmer and less seasonally variable temperatures than other tetrapod groups (Fig. 6). Previous studies have linked pseudosuchian, specifically crocodylomorph, diversity with palaeoclimate (Markwick 1998; Carvalho *et al.* 2010; Martin *et al.* 2014; Mannion *et al.* 2015; Shirley & Austin 2017; de Celis *et al.* 2019). Even today, modern crocodylomorphs exhibit relatively narrow temperature ranges and temperature greatly affects their feeding and reproductive strategies (Grigg & Kirshner 2015).

Similar to archosauromorphs and pseudosuchians, temnospondyls generally occupy warmer areas with low seasonal variation in temperature and precipitation (Fig. 6). Previous studies of metoposaurid temnospondyls and phytosaurs (members of Pseudosuchia) have noted that these groups have similar, but not identical, palaeolatitudinal distributions and are notably rare in the southern hemisphere during the Late Triassic (Buffetaut 1993; Brusatte *et al.* 2013; Stocker & Butler 2013; Barrett *et al.* 2020). In particular, the absence of phytosaurs from well-sampled deposits in Argentina and South Africa is hypothesized to have been linked to local climate conditions in south-western Pangea (Brusatte *et al.* 2013), and this hypothesis could explain the absence of metoposaurids in the same faunas (Brusatte *et al.* 2015; but see Barrett *et al.* 2020). Our results broadly support this hypothesis, suggesting that temnospondyls were constrained in the range of palaeoclimatic conditions they occupy (Fig. 6).

Avemetatarsalia, the archosaur group containing dinosaurs, has the largest range in both mean annual temperature and precipitation compared with the other groups, and it appears that the group occupies distinct palaeoclimatic ranges when compared to other archosauromorphs, particularly with regard to mean annual temperature and seasonality (Fig. 6). Dinosaur diversity has also previously been linked to climate (Benson *et al.* 2012; Mannion *et al.* 2012; Whiteside *et al.* 2015; Bernardi *et al.* 2018), but how this link developed at the very beginning of dinosaur evolution remains uncertain. One hypothesis is

TABLE 4. Summary of explanatory variables within the GLS multiple regression models for palaeolatitudinal coverage rarified species richness as indicated in Table 3.

Regression model	Intercept			MAT			MAP		
	Slope	SE	p	Slope	SE	p	Slope	SE	p
Null model	3.137	0.196	<0.001	–	–	–	–	–	–
MAT	0.942	0.853	0.312	0.711	0.269	0.039	–	–	–
MAP	6.422	1.510	0.005	–	–	–	−4.031	1.723	0.058
MAT + MAP	2.975	1.038	0.035	0.811	0.208	0.011	−2.819	1.088	0.049

Significant values are in **bold**.

MAP, mean annual precipitation; MAT, mean annual surface temperature.

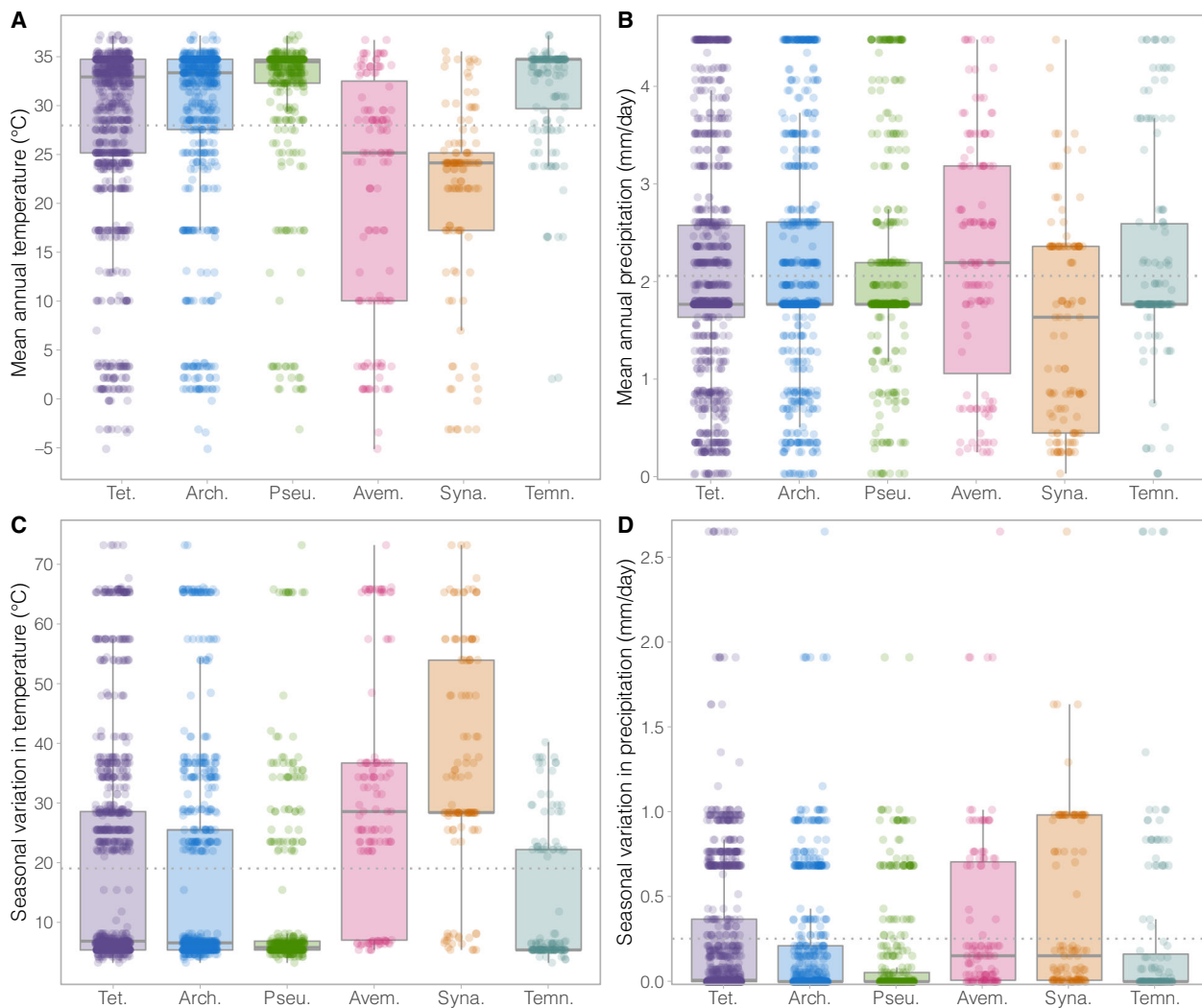


FIG. 6. Visualization of the palaeoclimatic conditions associated with each subgroup. Each dot represents a single occurrence of a species (note, the horizontal spacing of dots is random). Horizontal dotted lines indicate the mean value for all tetrapods. Climate variables: A, mean annual surface temperature; B, mean annual precipitation; C, seasonal variation in temperature; D, seasonal variation in precipitation. *Abbreviations:* Tet., all Tetrapoda; Arch., Archosauromorpha; Pseu., Pseudosuchia; Avem., Avemetatarsalia; Syna., Synapsida; Temn., Temnospondyli.

that the early diversification of dinosaurs may have been driven by the Carnian Pluvial Event, a period of increased rainfall that led to increased humidity compared to the generally arid conditions of the Late Triassic, and which is a proposed driver for the hypothesized Carnian–Norian extinction event (Benton *et al.* 2018; Bernardi *et al.* 2018; Dal Corso *et al.* 2018). Testing this hypothesis has been difficult due to the lack of detailed palaeoclimatic data for this event, particularly in regions where there are substantial dinosaur occurrences (Mancuso *et al.* 2020). Our finding that avemetarsalians (including early dinosaurs) occur over a wide range of mean annual temperature and precipitation values, in addition to the GLS results suggesting that models containing precipitation have little

explanatory power, calls into question the suggestion that the climatic conditions brought on by the Carnian Pluvial Event may have had a major impact on early dinosaur diversity.

The differences in palaeoclimatic conditions occupied by pseudosuchians and avemetatarsalians may be indicative of differences in thermal physiology. The more restricted palaeoclimatic range of pseudosuchians (Fig. 6) is analogous to modern day reptilian ectotherms (‘cold-blooded’ animals) that rely on their environment for temperature regulation. Conversely, avemetatarsalians exhibit comparatively wider ranges in occupied palaeoclimatic conditions (Fig. 6), which is more similar to endotherms (‘warm-blooded’ animals), such as birds and mammals.

This pattern exhibited by avemetarsalians is also more comparable to synapsids than to any other archosaur group within our dataset (Fig. 6). Thermal physiology is a central, and as yet unresolved, issue in dinosaur biology (Benson 2018). Early authors suggested that dinosaurs, like other reptiles, were ectothermic, while others have hypothesized that dinosaurs were endothermic on account of their proposed active lifestyle and high metabolic rates (Sander *et al.* 2011; Eagle *et al.* 2015). Other workers have suggested that dinosaurs may have been mesothermic, an intermediate physiology where their metabolic rates were elevated when compared with other reptiles but did not match those of extant mammals and birds (Grady *et al.* 2014; Eagle *et al.* 2015). Our data show that avemetarsalians (including early dinosaurs) occurred across a wide range of temperatures and levels of precipitation, suggesting that they were probably not constrained in their distribution by climatic conditions, which is consistent with an endothermic or mesothermic condition. While it is beyond the scope of this investigation to confirm this, the overall range of palaeoclimatic conditions occupied by Late Triassic archosauromorphs does not suggest that species were constrained in their global distribution by climate.

Our GLS analysis did not capture a clear relationship between species richness (both face-value richness and coverage-rarified richness) and palaeoclimate. Instead, the best models all featured the sampling proxy (TBCs) as an explanatory variable, suggesting that sampling is the major determinant of observed patterns of spatial species richness during the Late Triassic. This finding is consistent with the similar analyses performed on time-series data for lepidosaurs (Cleary *et al.* 2018), marine reptiles (Benson & Butler 2011), dinosaurs (Benson & Mannion 2012; Mannion *et al.* 2012) and pterosaurs (Butler *et al.* 2013), which also found the number of tetrapod-bearing collections as either the best explanatory variable, or the best in conjunction with non-marine area and/or the presence of Lagerstätten (another proxy for sampling). Nonetheless, the next best models in our face-value species richness GLS featured MAT or MAP in addition to sampling (Table 1), and a correlation between coverage-rarified species richness and palaeoclimate was also recovered (Table 3), suggesting that palaeoclimate may also have some role in driving diversity that was not fully captured in these statistical analyses.

Exploring the palaeoclimatic ranges of tetrapod groups using high resolution palaeoclimate reconstructions has allowed a greater insight into the influence of climatic conditions on the spatial distribution of these animals. Sampling heterogeneity will continue to impede studies of taxic palaeodiversity, therefore approaches that can more appropriately use palaeoclimate reconstructions instead of reducing the output down to single values for coarse

spatial bins should be favoured. Approaches such as ecological niche modelling (Chiarenza *et al.* 2019; Jones *et al.* 2019; Saupe *et al.* 2019) or those that incorporate phylogenetic relationships (Pie *et al.* 2017), with their ability to circumvent many issues associated with uneven and incomplete sampling, are promising avenues for investigations of the link between palaeoclimate and patterns of deep time diversity. The work presented here could be expanded by using the approach of Chiarenza *et al.* (2019) and Saupe *et al.* (2019), in which suitable habitat is modelled via ecological niche modelling using palaeoclimate reconstructions, ultimately illuminating the role of palaeoclimate in driving changes in the geographical distribution of species while reducing the dependence on raw occurrence data.

CONCLUSION

For most Late Triassic tetrapod groups, species richness was found to be highest at mid-palaeolatitudes. However, pseudosuchians (crocodylans and their relatives) exhibited a modern-type gradient in diversity, a pattern that is retained throughout their evolutionary history (Mannion *et al.* 2015). Statistical analyses could not confirm a clear relationship between palaeolatitudinal species richness and palaeoclimatic conditions, informed by palaeoclimatic reconstructions from the general circulation model HadCM3L. Instead, sampling appears to be the primary driver of the spatial (and palaeolatitudinal) distribution of Late Triassic tetrapods, despite the Late Triassic being comparatively better sampled across palaeolatitudes than neighbouring intervals. However, there is still evidence to suggest that the palaeoclimatic ranges of certain tetrapod groups were constrained. The differences in palaeoclimatic ranges occupied by pseudosuchians and those of avemetarsalians (the lineage leading to dinosaurs), which had comparatively wider ranges, may be indicative of differences in thermal physiology between the two groups.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5ps>), https://github.com/emmadunne/pbdb_cleaning and <http://www.bridge.bris.ac.uk/resources/simulations>. This is Paleobiology Database official publication number 383.

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